

Comparing different floral resources on the longevity of a parasitic wasp

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- Abstract**
- 1 The effects of floral resources of several important non-crop host plants of *Lygus lineolaris* on the longevity of *Anaphes iole*, one of its natural enemies, was studied.
 - 2 Median longevity of *A. iole* wasps provisioned with floral resources (*Erigeron annuus*, *Oenothera speciosa*, *Lamium amplexicaule*, and *Capsella bursa-pastoris*) was in the range 1.27–3.24 days, and did not differ from wasps in the distilled water only control (1.46–2.81 days), but was less than median longevity of wasps provisioned with distilled water + sucrose (5.30–12.46 days). No difference in longevity was observed between gender, although females usually lived slightly longer than males.
 - 3 High-performance anion-exchange chromatography analyses of *O. speciosa* floral nectar revealed that the major carbohydrate components were sucrose, glucose, and fructose.
 - 4 The results indicate that the floral resources of some non-crop plants that serve as important reproductive hosts for *L. lineolaris* offer little or no benefit to *A. iole*.

Keywords *Anaphes iole*, biological control, carbohydrates, floral resources, high-performance anion-exchange chromatography, *Lygus*, nectar, pollen.

Introduction

Parasitic wasps regulate herbivore populations and pollinate plants, and are thus valuable components of agroecosystems (Quicke, 1997). Many parasitic wasps utilize floral resources, such as nectar and pollen, to satisfy energy requirements for maintenance and reproduction (Jervis *et al.*, 1993, 1996; Berndt & Wratten, 2005; Wäckers, 2005). In particular, parasitoid food sources can play a key role in enhancing parasitoid longevity (Jacob & Evans, 2000; Lee *et al.*, 2004; Irvin *et al.*, 2007) and reproduction (Irvin *et al.*, 2006; Irvin & Hoddle, 2007; Onagbola *et al.*, 2007), and regulation of host population dynamics (Jervis *et al.*, 1996; Sabelis *et al.*, 2005).

Anaphes iole Girault (Hymenoptera: Mymaridae) is an egg parasitoid that attacks pestiferous *Lygus* species as well as non-pest mirids in North America (Huber & Rajakulendran,

1988; Udayagiri *et al.*, 2000). Under laboratory conditions, the longevity of *A. iole* wasps is limited to less than 3 days in the absence of food, but can exceed 10 days when honey is provided (Jones & Jackson, 1990). This wasp is pro-ovigenic (but see Riddick, 2005a, b) and adults do not require a food source to mature eggs. Adult *A. iole* does not host feed, and field observations of feeding by this tiny wasp are lacking. Nevertheless, evidence suggests (Williams & Roane, 2007) that foraging by adult *A. iole* might lead to increased longevity and allow the wasp more time to search for and parasitize hosts, thereby leading to a possible increase in realized fecundity.

Lygus species are important pests of many crops in North America (Wheeler, 2001). In the southcentral U.S.A., spring populations of *Lygus lineolaris* (Palisot de Beauvois) increase on non-crop vegetation before dispersing to crops after spring hosts senesce (Snodgrass *et al.*, 1984). Important non-crop hosts include *Erigeron annuus* (Linnaeus) Persoon, *Oenothera speciosa* Nuttall, *Lamium amplexicaule* Linnaeus, and *Capsella bursa-pastoris* (Linnaeus) Medikus, which are

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widespread in the southcentral U.S.A. and are believed to contribute significantly to *L. lineolaris* populations that infest cotton (Snodgrass *et al.*, 1984). Recent work has demonstrated that destruction of spring host plants suppresses subsequent *L. lineolaris* densities in adjacent crop fields (Snodgrass *et al.*, 2005, 2006). However, the effect of vegetation management strategies on natural enemies of *L. lineolaris* is unknown. Vegetation management practices that eliminate an important food source for *A. iole* may reduce the ability of the wasp to suppress *L. lineolaris* populations that will inevitably establish in crop fields. It is possible that cultural control and biological control can work in concert to suppress *L. lineolaris* populations but this necessitates a better understanding of the effects of vegetation management strategies on natural enemies. The present study aimed to compare the survival of *A. iole* when provisioned with floral resources of non-crop plants important for spring population growth of *L. lineolaris*.

Materials and methods

Insects

Anaphes iole used in this study were obtained from a laboratory colony maintained on *L. hesperus* Knight eggs at the USDA-ARS Biological Control and Mass Rearing Research Unit, Mississippi State, Mississippi. Mixed-gender colonies of wasps were held in Plexiglass cages (26 × 26 × 20 cm) at 27 ± 1°C, 65–85% relative humidity (RH), and under an LD 14 : 10 h photoperiod until experimentation.

Longevity

The effect of floral resources of *E. annuus*, *O. speciosa*, *L. amplexicaule*, and *C. bursa-pastoris* on survival of *A. iole* wasps was evaluated in the laboratory. Due to differences in phenology between the plant species, it was impossible to set up a single trial with all species; instead, several trials were conducted when each of the plant species under study was at peak flowering in the field. Two controls consisting of: (i) distilled water only and (ii) distilled water + sucrose were included in each trial. This study evaluated the effect of *ad libitu* provision of floral resources on wasp survival. Each trial was set up as indicated below.

A bioassay unit consisted of a 946-mL transparent plastic food container (no. DM32, SOLO Cup Co., Urbana, Illinois) with a piece of white nylon mesh cut from women's hosiery (L'eggs Knee Highs, Sara Lee Hosiery, Rural Hall, North Carolina) as a lid (diameter 7.5 cm). Two pipet tips (30 µL) were inserted into small holes cut in the fabric. For the untreated control and nectar treatments, both pipet tips contained distilled water. For the water + sugar treatment, one pipet tip contained distilled water, and the other was filled with 1 M sucrose (≥ 99.5% purity, catalog no. 84097, Fluka Biochemika, Switzerland) solution prepared with distilled water. Pipet tips were replaced daily with fresh distilled water and sucrose. The bioassay units for floral treatments con-

tained three 15-cm long plant stems bearing flowers. The cut ends of the stems protruded through small holes in the bottom of the bioassay unit into plant nutrient solution (OASIS Clear Solution, Smithers-Oasis, Kent, Ohio), which was changed every other day. Stems were cut immediately before use from wild plants growing in the vicinity of the laboratory (Stoneville, MS; 33°25'27"N, 90°54'54"W) and were replaced every other day. Plants were selected that were apparently healthy, undamaged and free of honeydew-producing homopterans and mirid eggs. The characteristics of the plants used in the study are given in Table 1. Approximately 12 recently emerged (< 3 h) wasps of mixed gender were transferred into each bioassay unit. Mortality of male and female wasps attributed to handling was determined for each unit approximately 4 h after the trial was setup, and was subtracted from subsequent observations. Bioassay units were held in an environmental chamber (20 ± 1°C, 60–85% RH, LD 14 : 10 h photoperiod), and mortality of wasps in each unit was assessed daily at 30× magnification until all wasps had died. A total of 491 wasps was used in the study.

Bioassays were set up in a randomized complete block design with three replicates for each of the controls and ten replicates for the floral treatments. A serial sampling design was used, where survival of the entire group of wasps was followed through time (Robertson & Preisler, 1992). Longevity of wasps was analyzed as a function of time. Survival of *A. iole* was analyzed by probit analysis, including likelihood ratio tests of parallelism (for equal slopes) and equality (for equal slopes and intercepts; LeOra Software, 1987).

Chromatographic analysis of nectar

Oenothera speciosa floral nectar was collected in April and May from plants growing on roadsides and fallow fields in the vicinity of the laboratory. Collections were made during the morning (08.00–09.00 h CST) before nectar was removed by insects or altered by microbial activity. Nectar was collected in glass capillary tubes (15 µL, VWR Scientific, West Chester, Pennsylvania), placed in 70% ethanol, and held at –20 °C until analysis.

High-performance anion-exchange chromatography analysis (HPAEC; Hendrix & Wei, 1994; Wei *et al.*, 1996; Beach *et al.*, 2003) was used to identify the major carbohydrates

Table 1 Plant characteristics of species tested for effects of floral resources on longevity of *Anaphes iole* wasps

Species	Biomass per stem (g) ^a (mean ± SD)	No. flowers (mean ± SD)
<i>Erigeron annuus</i>	0.21 ± 0.05	12.9 ± 3.63
<i>Oenothera speciosa</i>	0.81 ± 0.26	6.40 ± 1.58
<i>Lamium amplexicaule</i>	0.20 ± 0.06	NR
<i>Capsella bursa-pastoris</i>	0.09 ± 0.02	NR

^aPlants were oven-dried at 70°C for 3 days prior to biomass measurement.

NR, Flowers present but not recorded.

present in floral nectar. Nectar samples were filtered on a RP-18 column (Merck & Co., West Trenton, New Jersey) before injection into the HPAEC, which consisted of a Dionex gradient pump and a pulsed electrochemical detector operated in the integrated amperometric mode. For carbohydrate separation, a Spectra Physics AS3500 autosampler (Mountain View, California) was programmed to inject 25 µL onto a Dionex CarboPac PA-1 guard column (4 × 50 mm inner diameter; Sunnyvale, California) followed by two Dionex CarboPac PA-1 (4 × 250 mm inner diameter) columns connected in series. Elution was programmed for 25 min at 1.0 mL/min with a 200 mM NaOH mobile phase and a sigmoidal gradient of 0 to 0.5 M NaOAc. Because detector response varies between individual sugars (Larew & Johnson, 1988), sample peaks were identified by comparing the retention time of known sugar standards with sample sugars.

Results

Longevity

Comparison of ST_{50} values (survival time for 50% of the study insects) indicated that provision with floral resources did not significantly increase survival of *A. iole* beyond the distilled water control (Table 2). However, survival of wasps provisioned with *O. speciosa*, *L. amplexicaule*, and *C. bursa-pastoris* was numerically, but not significantly, greater than the distilled water control. In all trials, survival of wasps in the distilled water + sucrose control was significantly greater than in other treatments. Maximum longevity was greater than 8 days for wasps provisioned with the distilled water + sucrose control (Fig. 1). For wasps provisioned with floral resources, maximum longevity was in the range 9–13 days (Fig. 1); these wasps represented less than 5% of the wasps in this treatment. Likelihood ratio tests of the slope for the *E. annuus* floral resource treatment was intermediate between the distilled water control and the distilled water + sucrose control ($\chi^2 = 15.75$, d.f. = 2, $P < 0.05$; Table 2, Fig. 1). Slopes for the *C. bursa-pastoris* and *L. amplexicaule* floral resource treatments were each significantly greater than the distilled water + sucrose control, but not the distilled water

control ($\chi^2 = 31.06$, d.f. = 3, $P < 0.05$; Table 2, Fig. 1). Furthermore, the slope for the *C. bursa-pastoris* floral resource treatment was significantly greater than for the *L. amplexicaule* floral resource treatment. In Trial 2 (*O. speciosa*), all slopes were equal ($\chi^2 = 5.10$, d.f. = 2, $P > 0.05$; Table 2, Fig. 1).

Chromatographic analysis of nectar

Gradient HPAEC analysis demonstrated that the major carbohydrate components of *O. speciosa* floral nectar were glucose, fructose, and sucrose (Fig. 2). Inositol and other unidentified minor components were also present.

Discussion

The floral resources used in this study did not significantly extend the lifespan of *A. iole* wasps. These results suggest that either floral resources suitable to *A. iole* are not present in the plant species included in the study, or that suitable resources are present but inaccessible to the wasps. Examination of plant stems under a dissecting scope (× 20–50) revealed that *E. annuus*, *L. amplexicaule*, and *C. bursa-pastoris* had partially-hidden nectaries that probably afforded limited access to *A. iole*, although pollen was present in all species. However, *O. speciosa* had exposed floral nectaries that produced glucose, fructose, and sucrose. In gustatory acceptance studies, Beach *et al.* (2003) demonstrated that these carbohydrates are readily fed on by *A. iole* at a wide range of concentrations. Williams & Roane (2007), found that *A. iole* wasps rapidly metabolized ingested sucrose, and that longevity of wasps provisioned with sucrose, glucose, and fructose was increased by more than three-fold compared with wasps in distilled water controls. These sugars are also important food sources for many other parasitoids (Azzouz *et al.*, 2004; Fadamiro *et al.*, 2005; Wäckers, 2001, 2005; Winkler *et al.*, 2005). Pollen is an important food for some parasitoids (Leius, 1963; Haslett, 1989; Jervis *et al.*, 2004; Wäckers, 2005), but did not appear to benefit *A. iole* in the present study, and no examples of other mymarids feeding on pollen are known. Floral resource provisioning enhanced

Table 2 Regression analysis of effects of nectar on longevity of *Anaphes iole* wasps

Trial no.	Food source	ST_{50} days (95% CI) ^a	Slope ± SE ^b	χ^2	d.f.
1	Distilled water	1.805 (1.553–2.050)	−5.44 ± 0.80 ^A	1.47	3
1	Distilled water + sucrose (1 M)	10.48 (8.508–14.90)	−2.23 ± 0.38 ^C	3.24	9
1	Distilled water + <i>Erigeron annuus</i>	1.274 (0.699–1.694)	−3.47 ± 0.34 ^B	9.30	3
2	Distilled water	1.464 (1.045–1.953)	−1.97 ± 0.37 ^A	1.70	2
2	Distilled water + sucrose (1 M)	5.301 (4.286–7.391)	−2.90 ± 0.48 ^A	7.16	6
2	Distilled water + <i>Oenothera speciosa</i>	2.362 (1.255–3.701)	−1.77 ± 0.19 ^A	22.6	5
3	Distilled water	2.812 (2.439–3.211)	−4.26 ± 0.61 ^{AB}	2.28	4
3	Distilled water + sucrose (1 M)	12.46 (10.44–16.07)	−1.98 ± 0.27 ^C	10.4	13
3	Distilled water + <i>Lamium amplexicaule</i>	3.242 (2.725–3.760)	−3.18 ± 0.26 ^B	12.7	7
3	Distilled water + <i>Capsella bursa-pastoris</i>	3.226 (2.629–3.867)	−4.51 ± 0.44 ^A	13.1	5

^a ST_{50} values (survival time for 50% of the study insects) with overlapping 95% confidence intervals (CI) are not significantly different.

^bFor each trial, slopes that are not significantly different are followed by the same uppercase letter.

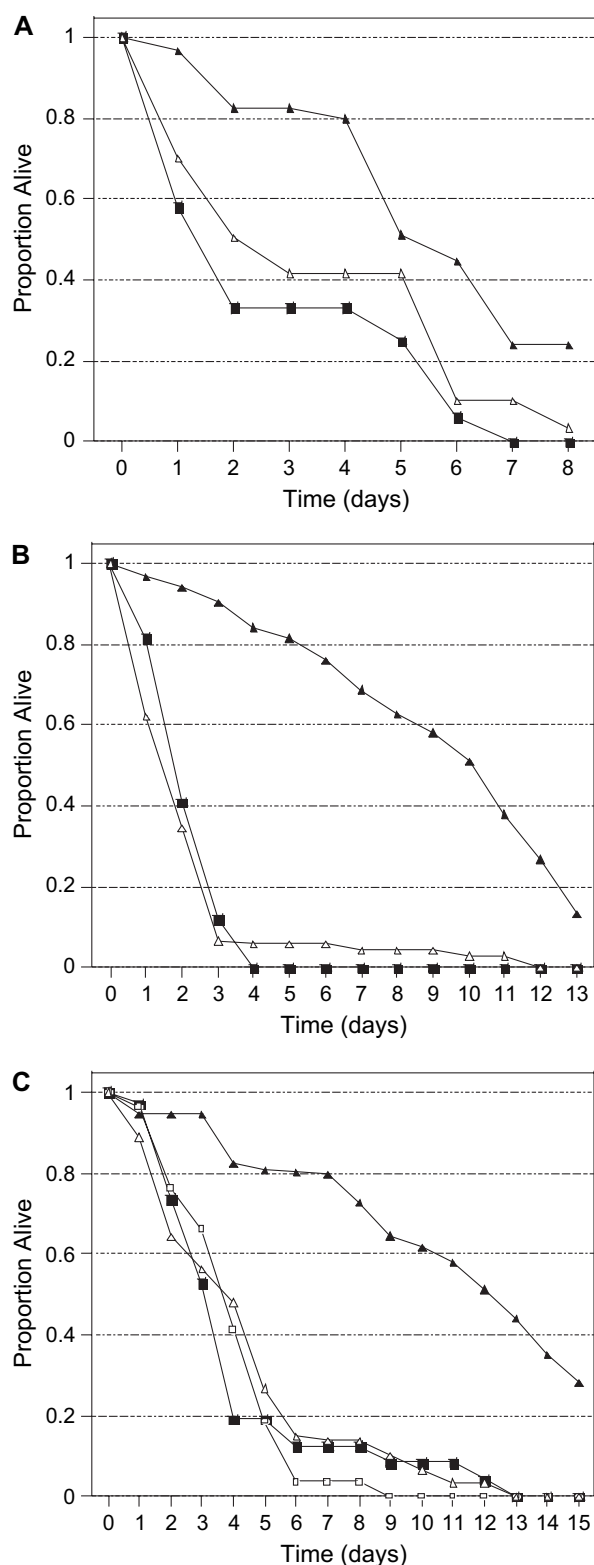


Figure 1 Effect of floral resources on survival of *Anaphes iole* wasps. (A) *Oenothera speciosa* (Δ); (B) *Erigeron annuus* (Δ); (C) *Capsella bursa-pastoris* (□), *Lamium amplexicaule* (Δ). ■, Distilled water; ▲, distilled water + sucrose (1 M).

longevity and fitness of three other mymarid species (Irvin & Hoddle, 2007; Irvin *et al.*, 2007). Life-history traits, longevity and fitness of *Gonatocerus ashmeadi*, *Gonatocerus triguttatus*, and *Gonatocerus fasciatus* were enhanced to various degrees by floral resources of five plant species being considered as candidates for understory management. Although these were different plant species from those of the present study, the major carbohydrate components of their nectar was fructose, glucose, and sucrose, as was the case for *O. speciosa*. Thus it appears that floral resources may have differential effects on parasitoids that are closely related and with similar life histories.

It is interesting that survival of *A. iole* was poor on *O. speciosa*, given that this plant produces floral nectar with sugars utilized by this wasp. It is unlikely that glucose, fructose, and sucrose in *O. speciosa* nectar occur at concentrations undetected by *A. iole* because the wasp's range of gustatory responses to these sugars is quite broad (Beach *et al.*, 2003), and encompasses the concentrations at which sugars usually occur in nectar (Baker & Baker, 1983a, b; Koptur, 2005). Accessibility of nectar to parasitoids is an important factor affecting floral resource suitability (Patt *et al.*, 1997; Wäckers, 2004, 2005) but, considering the minute size of *A. iole* (approximately 0.8 mm length) and the exposed nectaries of *O. speciosa*, restricted access to nectar is an unlikely explanation. It is possible that using excised flowers altered floral resources such that they were not beneficial to *A. iole* wasps. Wade and Wratten (2006) reported that flower presentation method (excised versus intact flowers) usually did not affect the longevity of *Aphidius ervi*, and cautiously recommended use of excised inflorescences in future studies. In the present study, floral resources were replaced every other day, and it is unlikely that the nectar that was present when the flowers were excised would have disappeared or been altered before being fed on by *A. iole*. It is also unlikely that wasps suffered a reduced lifespan due to

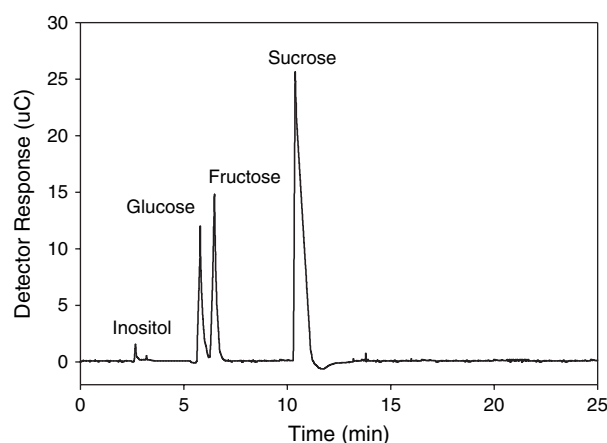


Figure 2 Sodium acetate-gradient high-performance anion-exchange chromatography analysis of *Oenothera speciosa* floral nectar, showing major peaks of sucrose, fructose, and glucose.

repeated mating behaviour. *Anaphes iole* is protandrous, and males usually mate with females soon after the females emerge; observations made during the present study confirmed that wasps spent most time foraging, not mating. A possible explanation for our results may be related to chemical or physical characteristics of plants that deter insects from utilizing resources that would otherwise be suitable. For example, floral and extrafloral nectar is composed of many compounds (e.g. carbohydrates, amino acids, and secondary plant metabolites), some of which are deleterious to insects (Barker, 1990; Adler, 2001; Wäckers, 2001, 2005; Romeis & Wäckers, 2002; Liu *et al.*, 2007). Furthermore, plant-produced volatiles, such as nectar or floral odours (Patt *et al.*, 1997; Wäckers, 2004) or odours from vegetative tissue (Bukovinszky *et al.*, 2005; Lou *et al.*, 2005), may influence parasitoid behaviour, in turn affecting propensity for nectar feeding. The presence of secondary metabolites in pollen has been attributed to its toxicity to some insects (Yue & Tsai, 1996; Wäckers, 2005). Therefore, it is possible that *O. speciosa* has characteristics that adversely affect the behaviour or physiology of *A. iole*, thereby limiting the suitability of its nectar to this wasp.

Identifying and characterizing the complex effect of foods is important for understanding insect–plant interactions, and has direct implications for biological control programmes (Begum *et al.*, 2006). The findings of the present study reiterate the importance of understanding the interplay between the chemical composition of food sources and their availability, apparency, and accessibility with respect to the nutrition of parasitic insects (Gurr *et al.*, 2004; Wäckers, 2005). The results suggest that *E. annuus*, *L. amplexicaule*, *C. bursa-pastoris*, and *O. speciosa*, all important reproductive hosts of *L. lineolaris*, do not represent meaningful food sources for *A. iole*. However, other effects of vegetation management on the wasp must be evaluated to fully understand the influence of such practices on *A. iole* populations. Effective integration of biological and cultural control for suppression of *L. lineolaris* will require improved knowledge of population dynamics of natural enemies, especially *A. iole* population development after vegetation management that destroys wasps developing in host eggs.

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